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A TAXONOMIC REVIEW OF SOUTH AMERICAN  
HYLID FROGS, GENUS *PHRYNOHYAS*

By

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Few large South American hylid frogs are so poorly known taxonomically as the widespread *Phrynohyas venulosa* (Laurenti, 1768) and its congeners. Duellman (1956) included three South American species in the genus; four other species were recognized in Central America and México. Duellman (1966) and McDiarmid (1968) reduced all of the Middle American nominal species to synonyms of *Phrynohyas venulosa*. Duellman (1968) resurrected *Hyla coriacea* Peters from the synonymy of *Phrynohyas venulosa* and showed that *coriacea* was a valid species of *Phrynohyas* in the Guianas and Amazon Basin. Bokermann (1966) listed *Hyla mesophaea* Hensel and *Hyla imitatrix* Miranda-Ribeiro in the genus *Phrynohyas*.

The purposes of the present paper are to: 1) redefine the hylid genus *Phrynohyas*, 2) describe the geographic variation in the widespread *Phrynohyas venulosa*, 3) ascertain the assignments of several nominal species, and 4) present a synopsis of the species in the genus.

Specimens examined are designated by the following abbreviations of depositories:

- |        |   |
|--------|---|
| AMNH   | American Museum of Natural History  |
| ANSP   | Academy of Natural Sciences, Philadelphia                                 |
| BMNH   | British Museum (Natural History)  |
| CAS    | California Academy of Sciences  |
| CAS-SU | Stanford University collection, now in the California Academy of Sciences |
| FMNH   | Field Museum of Natural History   |

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IRSNB	Institut Royal des Sciences Naturelles Belgique
KU	University of Kansas Museum of Natural History
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard
MLS	Museo de La Salle, Bogotá
MJP	Museo Javier Prado, Lima
MNHN	Museum National d'Histoire Naturelle, Paris
MNRJ	Museu Nacional, Rio de Janeiro
MZUSP	Museu de Zoologia, Universidade de São Paulo
NHMG	Naturhistoriska Museet, Göteborg
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
RMNH	Riksmuseet van Natuurlijke Histoire, Leiden
SMF	Senckenbergische Museum, Frankfurt
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
UZM	Universitets Zoologiske Museum, Copenhagen
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZIUS	Zoologiske Institut, Universitet Stockholm
ZMB	Zoologisches Museum, Berlin
ZSM	Zoologisches Staatssammlung, Munich

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#### PHRYNOHYAS FITZINGER, 1843

*Phrynohyas* Fitzinger, 1843:30 [type species, *Hyla zonata* Spix, 1824 (= *Rana venulosa* Laurenti, 1768) by monotypy and declaration of International Commission on Zoological Nomenclature (Opinion No. 520, 1958)].

*Acrodytes* Fitzinger, 1843:30 [type species, *Hyla venulosa* Daudin, 1803 (= *Rana venulosa* Laurenti, 1768) by monotypy; generic name suppressed by International Commission on Zoological Nomenclature (Opinion No. 520, 1958) for purposes of Law of Priority, but not for those of Law of Homonymy].

*Scytotis* Cope, 1862:354 [type species, *Scytotis hebes* Cope, 1862, by monotypy].

*Diagnostic Definition.*—1) Skull slightly broader than long; 2) dermal roofing bones of skull well ossified, lacking exostosis and co-ossification; 3) nasals broad, overlapping anterior edge of sphenethmoid, not articulating with maxillaries; 4) frontoparietals having complete medial articulation, entirely covering frontoparietal fontanelle; posterolateral margin of frontoparietal lying just medial to epiotic eminence; 5) sphenethmoid well ossified with large portion exposed dorsally; 6) maxillary arch complete; pars facialis of maxillary moderately well developed but not articulating with nasal; 7) squamosal weakly articulating with prootic; zygomatic ramus extending about one-half of distance to maxillary; 8) pterygoid robust with complete articulations; 9) dentigerous processes of pre-momers curved; 10) parasphenoid large, edentate, acuminate anteriorly; alae oriented posterolaterally; 11) palatines moderately large, widely separated medially, bearing dentigerous ridge; 12) neural arches of vertebrae low, non-imbricate; 13) transverse processes of vertebrae subequal in width; width of processes on third presacral vertebra less than width of sacral diapophyses; 14) sacral diapophyses expanded; 15) ilial shaft long, cylindrical, with low dorsal protuberance; 16) pubis cartilaginous; 17) clavicles expanded distally, strongly arched; 18) coracoids expanded distally and proximally, widely separated medially; 19) epicoracoids broadly overlapping; 20) suprascapula large, well ossified; cleithrum ossification incorporated into suprascapula; 21) vocal sacs paired, lateral, behind angles of jaws; 22) submentalis muscle moderate in size, araphic; 23) intermandibularis muscle undifferentiated, lacking aponeurosis; 24) interhyoideus muscle forming large supramandibular lobes; no myointegumental contact between lobes and sacs; 25) postmandibular septum short, attached to posterior end of intermandibular portion of interhyoideus; 26) length of vocal slits about one-fifth of length of mandible; 27) skin on dorsum thick, glandular, and smooth, granular, or tuberculate; that on venter heavily granular; 28) parotoid glands extensively developed in occipital and scapular regions; 29) diameter of tympanum 50-75 percent of diameter of eye; upper edge covered by supratympanic fold; 30) discs large, round; 31) fingers one-fourth to two-thirds webbed; toes about three-fourths webbed; 32) smooth, horny nuptial excrescences in breeding males; 33) pupil horizontal; 34) palpebrum clear; 35) snout-vent length of adults 50-114 mm; 36) known tadpoles having four upper and six lower rows of teeth.

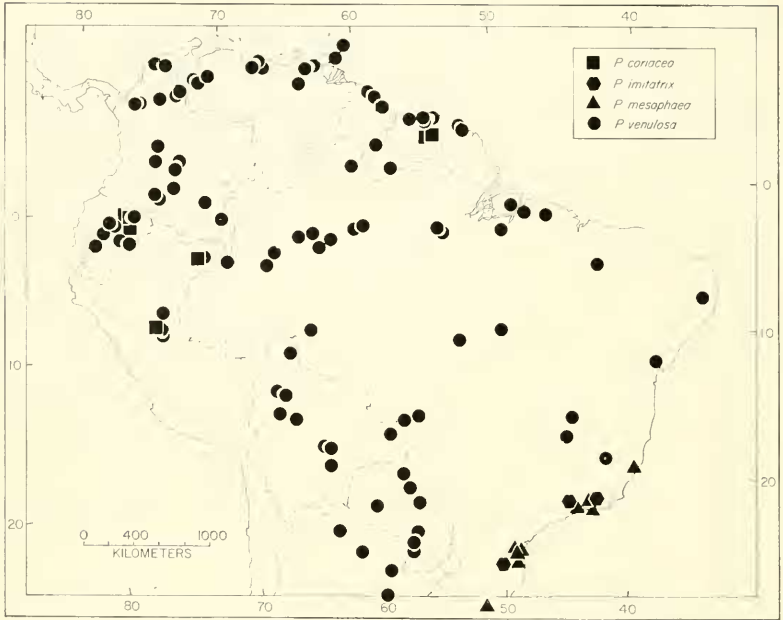


FIG. 1. Map showing locality records for the species of *Phrynohyas*.

*Content.*—As defined here, the genus contains four species: *P. coriacea* (Peters), *P. imitatrix* (Miranda-Ribeiro), *P. mesophaea* (Hensel), and *P. venulosa* (Laurenti, 1768).

*Distribution.*—The lowland tropics from Sinaloa and Tamaulipas, México, southward to Chaco, Entre Ríos, and Salta, Argentina, and Rio Grande do Sul, Brasil. The genus occurs on Trinidad and Tobago, but only two specimens are known from the Pacific lowlands of South America (Fig. 1). Most records of occurrence are at elevations of less than 500 m, but the frogs ascend the Amazonian slopes of the Andes to about 800 m and are known to occur at elevations of 1200 m in the Serra do Mar and Serra da Mantiqueira in southeastern Brasil.

*Comments.*—As pointed out by Trueb and Duellman (1971:38), only four hyloid genera have paired lateral vocal sacs; these are *Argenteohyla*, *Osteocephalus*, *Phrynohyas*, and *Trachycephalus*. Tyler (1971:349) provided evidence that the paired lateral vocal sacs were derived from single subgular sacs and stated: “Conceivably the very highly specialized vocal sacs of *Phrynohyas* and *Trachycephalus* could have been derived from the simpler structures now found in some species of *Osteocephalus*.” Trueb and Duellman (1971:40) concluded that *Phrynohyas* and *Trachycephalus* probably

were representatives of one phyletic line. *Trachycephalus* differs from *Phrynohyas* principally by having a heavily casqued, co-ossified skull and by lacking extensive parotoid glands.

## GEOGRAPHIC VARIATION IN *PHRYNOHYAS VENULOSA*

In 1956 I noted the presence of variation in size and coloration in *P. venulosa* in the Amazon Basin; furthermore, I recognized, taxonomically two peripheral populations—*P. hebes* in the Gran Chaco and *P. ingens* in the Maracaibo Basin. Examination of many additional South American specimens reveals that the mosaic of variation is more complex than that described previously.

*Size.*—In South America very large individuals of *P. venulosa* occur in the Maracaibo Basin (females to 112.5 mm in snout-vent length) and in Amazonian Ecuador (females to 110.2 mm in snout-vent length). Equally large individuals are known from Panamá and Costa Rica (Duellman, 1970:165). Specimens from other areas in South America are noticeably smaller (Table 1). Measurements and proportions of the limbs and head all are positively correlated with snout-vent length. Duellman (1956) suggested that there were interpopulational differences in the size of the tympanum, but data from larger series of specimens negate that suggestion (Table 1). Also, there seems to be no correlation between size and habitat, as suggested by McDiarmid (1968).

*Skin.*—Considerable variation is apparent in the thickness and texture of the dorsal skin. Most specimens have scattered pustules dorsally; these are especially noticeable in young individuals. In a few specimens, such as KU 126067 from 2 km east of Leticia, Colombia, and especially MNRJ 4054 from Rio Branco, Brasil, the skin on the dorsum is highly pustulate. The parotoid glands result in thickened skin in occipital and scapular regions in most specimens from throughout the range. Many specimens from the upper Amazon Basin in Ecuador, Perú, and Bolivia have thick, leathery skin. McDiarmid (1968) suggested that extensive development of the parotoid glands is a seasonal phenomenon in frogs living in regions having wet and dry seasons, the glands being better developed in the dry season. Dates of collection are not available for many South American specimens of *P. venulosa*; the specimens having such data do not provide strong evidence in support of McDiarmid's proposal. For example, well-developed glands are evident in specimens from the upper Amazon Basin where there is no prolonged dry season;

TABLE 1.—Variation in Certain Measurements in *Phrinothias venulosa*.  
Measurements are in millimeters; means are given in parentheses below observed ranges.

Locality	N		Snout-vent Length		Tympanum Length	
	♂	♀	♂	♀	♂	♀
Trinidad	25	6	67.0-82.0 (74.9)	65.0-72.5 (67.8)	4.0-6.0 (4.8)	4.0-4.5 (4.7)
Venezuela: Maracaibo Basin	4	4	75.0-88.0 (84.0)	94.5-112.5 (101.4)	4.5-6.0 (5.3)	6.1-7.0 (6.6)
Brasil: Belém	7	3	58.5-75.3 (66.3)	63.1-68.9 (66.6)	3.9-4.7 (4.4)	4.1-4.7 (4.4)
Colombia: Leticia	5	-	63.9-70.5 (69.2)	-	4.7-5.0 (4.8)	-
Ecuador: Napo-Pastaza	7	3	84.8-92.5 (87.7)	102.8-110.2 (107.6)	5.6-7.4 (6.8)	8.1-9.1 (8.6)
Bolivia: El Beni	7	5	67.5-73.5 (70.9)	71.0-74.5 (73.1)	5.0-5.5 (5.1)	5.0-5.5 (5.1)
Bolivia: Santa Cruz	5	8	65.0-76.0 (69.0)	59.5-88.5 (73.0)	4.5-5.0 (4.7)	4.0-6.0 (4.8)
Paraguay	7	6	64.2-86.0 (78.7)	68.0-89.1 (81.0)	3.8-5.5 (4.9)	5.0-6.2 (5.6)

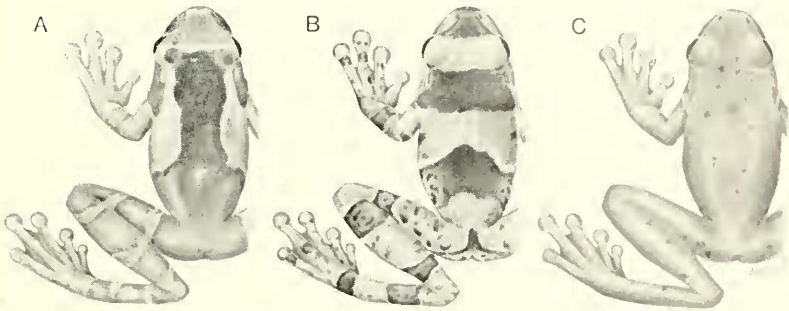


FIG. 2. Dorsal color patterns in *Phrynohyas venulosa*. A. Normal, code 4, KU 92258. B. Divided, code 3, KU 126067. C. Spotted, code 2, NIMW 19013 (holotype of *Hyla wettsteini*).

specimens from Napo and Pastaza provinces in Ecuador have more extensive glands than do individuals from the xeric Maracaibo Basin.

**Coloration.**—All individuals of *P. venulosa* are brown or tan dorsally with or without darker markings. The venter is uniform grayish white or pale tan. The iris is golden with radiating black lines. There is considerable variation in dorsal color pattern, but most of the variants can be grouped into one of four categories; code numbers indicate a decreasing amount of dark pigment dorsally (Fig. 2):

**NORMAL:** A large middorsal dark blotch extending from the occiput to the rump; blotch divided anteriorly by a longitudinal band of ground color in some specimens (coded 4).

**DIVIDED:** As above, but blotch divided by a broad transverse band of ground color (coded 3).

**SPOTTED:** Dorsal pattern consisting of irregular small dark spots (coded 2).

**PLAIN:** Dorsum uniform brown (coded 1).

The various color patterns are found throughout most of the range of the species in South America (Table 2). The only region in which all specimens have the normal pattern is Paraguay; the next highest percentage of specimens having the normal pattern is Trinidad (93%). All four color pattern types were found in only four of 14 pooled samples; normal and plain patterns occurred in 12 samples, and divided and spotted patterns occurred in eight samples. In the only large sample (151 specimens from Maracay, Venezuela) the following percentages occur: normal 14.6, divided 44.3, spotted 7.9, and plain 33.2. Each of the various patterns has been found in males, females, and juveniles. All four patterns, save the spotted one, are found in Central America.

TABLE 2.—Variation in Dorsal Color Pattern in *Phrynohyas venulosa*.  
See text for explanation of patterns and scoring.

Locality	N	Normal	Divided	Spotted	Plain	Score
Trinidad .....	32	30	1	1	0	3.91
Venezuela: Maracaibo Basin .....	8	0	0	7	1	1.89
Venezuela: Maracay .....	151	22	67	12	50	2.38
Surinam .....	21	15	0	2	4	3.28
Brasil: Belém .....	26	23	1	0	2	3.73
Brasil: Mato Grosso .....	15	2	0	12	1	2.20
Brasil: Manaus .....	8	3	3	0	2	2.87
Colombia: Leticia .....	5	1	1	0	3	2.00
Ecuador: Napo-Pastaza .....	13	0	1	0	12	1.25
Perú: Pebas .....	10	4	0	4	2	2.60
Perú: Pucallpa .....	12	6	0	0	6	2.50
Bolivia: El Beni .....	16	1	1	2	12	1.44
Bolivia: Santa Cruz .....	15	4	1	3	7	2.13
Paraguay .....	14	14	0	0	0	4.00

*Remarks.*—It is evident that the various characters considered to be of taxonomic value in this group vary independently of one another in *P. venulosa*. Refined quantitative analysis must await the acquisition of large series of specimens from throughout the range of the species. Currently, karyological, larval, and biosonic data are

TABLE 3.—Alphabetical Synonymy of the Species of *Phrynohyas*.

Trivial Name, Original Generic Name, Author, and Date	Current Name
<i>adenoderma</i> ( <i>Hyla</i> ) Lutz, 1968 .....	<i>P. venulosa</i>
<i>bufona</i> ( <i>Hyla</i> ) Spix, 1824 .....	<i>P. venulosa</i>
<i>corasterias</i> ( <i>Phrynohyas</i> ) Shamon and Humphrey, 1957 .....	<i>P. venulosa</i>
<i>coriacea</i> ( <i>Hyla</i> ) Peters, 1867 .....	<i>P. coriacea</i>
<i>hebes</i> ( <i>Scytopsis</i> ) Cope, 1862 .....	<i>P. venulosa</i>
<i>imitatrix</i> ( <i>Hyla</i> ) Miranda-Ribeiro, 1926 .....	<i>P. imitatrix</i>
<i>inflata</i> ( <i>Acrodytes</i> ) Taylor, 1944 .....	<i>P. venulosa</i>
<i>ingeus</i> ( <i>Phrynohyas</i> ) Duellman, 1956 .....	<i>P. venulosa</i>
<i>latifasciata</i> ( <i>Phrynohyas</i> ) Duellman, 1956 .....	<i>P. venulosa</i>
<i>lichenosa</i> ( <i>Hyla</i> ) Günther, 1859 .....	<i>P. venulosa</i>
<i>macrotis</i> ( <i>Hyla</i> ) Andersson, 1945 .....	<i>P. venulosa</i>
<i>mesophaea</i> ( <i>Hyla</i> ) Hensel, 1867 .....	<i>P. mesophaea</i>
<i>modesta</i> ( <i>Acrodytes</i> ) Taylor and Smith, 1945 .....	<i>P. venulosa</i>
<i>nigropunctata</i> ( <i>Hyla</i> ) Boulenger, 1882 .....	<i>P. venulosa</i>
<i>paenulata</i> ( <i>Hyla</i> ) Brocchi, 1879 .....	<i>P. venulosa</i>
<i>palpebrogranulata</i> ( <i>Hyla</i> ) Andersson, 1906 .....	<i>P. venulosa</i>
<i>quadrangulum</i> ( <i>Hyla</i> ) Boulenger, 1882 .....	<i>P. coriacea</i>
<i>resinifictrix</i> ( <i>Hyla</i> ) Goeldi, 1907 .....	<i>P. venulosa</i>
<i>spilomma</i> ( <i>Hyla</i> ) Cope, 1877 .....	<i>P. venulosa</i>
<i>venulosa</i> ( <i>Rana</i> ) Laurenti, 1768 .....	<i>P. venulosa</i>
<i>vermiculata</i> ( <i>Hyla</i> ) Duméril and Bibron, 1841 .....	<i>P. venulosa</i>
<i>wettsteini</i> ( <i>Hyla</i> ) Ahl, 1933 .....	<i>P. venulosa</i>
<i>zernyi</i> ( <i>Hyla</i> ) Ahl, 1933 .....	<i>P. venulosa</i>
<i>zonata</i> ( <i>Hyla</i> ) Spix, 1824 .....	<i>P. venulosa</i>



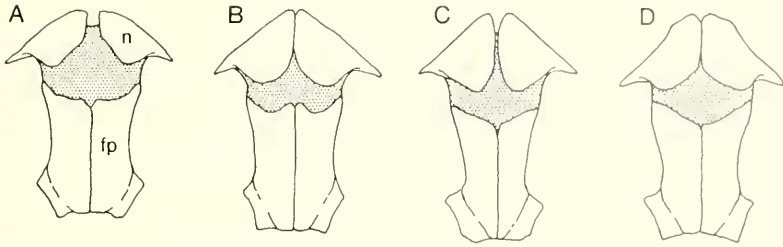


FIG. 3. Anterior cranial roofing bones showing positions of nasals and proportion of dorsal exposure of the sphenethmoid. A. *P. coriacea*, KU 105249. B. *P. imitatrix*, KU 92249. C. *P. mesophaea*, KU 92257. D. *P. venulosa*, KU 138830.

Abbreviations: fp = frontoparietal, n = nasal; sphenethmoid is stippled.

lacking. Until such data are available for a more sophisticated analysis, we must be content to base conclusions on the present inadequate series of preserved specimens, which have formed the basis for my broad definition of *Phrynohyas venulosa*.

### TAXONOMY OF PHRYNOHYAS

Data taken from series of preserved specimens, some living frogs, skeletal preparations, and radiographs provide a basis for the recognition of four species in the genus *Phrynohyas* (Table 3). Diagnostic external morphological characters and features of coloration are used in the following key. Osteological characters that are important at the species level are discussed below.

*Nasals*.—The size and position (relative to one another) of the nasals are distinctive (Fig. 3). In *P. imitatrix* and *venulosa* the nasals are juxtaposed; in *mesophaea* they are narrowly separated, and in *coriacea* they are widely separated.

*Sphenethmoid*.—The sphenethmoid is well ossified in all species. The proportion of the element exposed dorsally shows interspecific differences (Fig. 3); the area of exposure is dependent on the relative sizes and positions of adjacent dermal roofing bones—the nasals anteriorly and the frontoparietals posteriorly. The sphenethmoid is least exposed in *P. imitatrix* and moderately exposed in *mesophaea* and *venulosa*. A relatively large area of the sphenethmoid is exposed in *coriacea*, in which the nasals are widely separated.

*Prevomers*.—The dentigerous processes are curved and separated medially in all species. The curvature is slight and the separation moderate in *P. imitatrix* and *venulosa*, slight and widely separated in *coriacea*, and strongly curved and narrowly separated in *mesophaea*.

*Sacral Diapophyses*.—The diapophyses are dilated in all species; this dilation is symmetrical in *P. mesophaea* and *venulosa* and asymmetrical (greater dilation posteriorly) in *imitatrix* and *coriacea*.

KEY TO THE SPECIES OF *Phrynohyas*

1. Dorsal quadrangular mark outlined with white and terminating in sacral region; thighs lacking dark transverse bars; black post-tympanic spot present; red "flash-colors" in life ..... *P. coriacea*  
 Dorsal quadrangular mark, if present, usually not outlined with white; thighs usually having dark transverse bars (if blotches present on dorsum); black post-tympanic spot absent; no red "flash-colors" in life ..... 2
2. Dorsum and flanks dark brown with broad cream dorsolateral stripe from eyelid to groin; limbs unicolor or faintly barred dorsally ..... *P. mesophaea*  
 Dorsal pattern variable, but lacking dorsolateral cream strips; limbs usually distinctly barred, if blotch present on dorsum .... 3
3. Dorsal markings consisting of large brown blotch anteriorly and usually round spots or blotches posteriorly, darkest peripherally; limbs with distinct dark brown, light bordered bars; dorsal skin distinctly tuberculate ..... *P. imitatrix*  
 Dorsal markings absent or consisting of large dark blotch (transversely divided in some) or small dark spots; limbs unicolor or barred, lacking light borders; dorsal skin variable ..... *P. venulosa*

*Phrynohyas coriacea* (Peters)

*Hyla coriacea* Peters, 1867:711 [syntypes, ZMB 5807 (3 specimens) from Surinam; H. Kappler collector].

*Hyla quadrangulum* Boulenger, 1882:367 [holotype, BMNH 1947.2.13.75 from "western Ecuador"; Mr. Fraser collector]. New synonymy.

*Phrynohyas coriacea*—Duellman, 1968:205.

*Distribution*.—Surinam and the upper Amazon Basin in Ecuador and Perú at known elevations of less than 500 m (Fig. 1). The record for Machala on the Pacific coast of Ecuador probably is erroneous. 29 specimens from 11 localities.

*Remarks*.—The three syntypes (ZMB 5807) were reported on by Duellman (1968). The holotype of *Hyla quadrangulum* (BMNH 1947.2.13.75) is an adult female having a snout-vent length of 57.5 mm and morphological characters which render it indistinguishable from *P. coriacea*. The color pattern consists of a dark brown quadrangular dorsal blotch faintly outlined with cream on a tan dorsum; the limbs are distinctly barred, and a dark post-tympanic spot is evident.

The type locality of "western Ecuador" cannot be taken seriously; several species contained in the Fraser collections supposedly from western Ecuador have been found subsequently only in the Amazon Basin and eastern slopes of the Andes.

### **Phrynohyas imitatrix** (Miranda-Ribeiro)

*Hyla imitatrix* Miranda-Ribeiro, 1926:77 [syntypes, MNRJ 154 (2 specimens) from Teresópolis, Rio de Janeiro, Brasil; Alipio de Miranda-Ribeiro collector].

*Phrynohyas mesophaea*—Bokermann, 1966:55.

*Distribution*.—Mountains of southeastern Brasil—Serra do Mar, Serra da Bocaina, and Serra da Mantiqueira—in the states of Rio de Janeiro, São Paulo, and Santa Catarina (Fig. 1); the known localities are at elevations between 800 and 1200 m. Eight specimens from three localities.

### **Phrynohyas mesophaea** (Hensel)

*Hyla mesophaea* Hensel, 1867:154 [holotype, ZMB 6810 from Porto Alegre, Rio Grande do Sul, Brasil; Reinhold Hensel collector].

*Phrynohyas mesophaea*—Bokermann, 1966:55.

*Distribution*.—Coastal lowlands of southeastern Brasil from Bahia to Rio Grande do Sul (Fig. 1). 259 specimens from 13 localities.

### **Phrynohyas venulosa** (Laurenti)

*Rana venulosa* Laurenti, 1768:31 [based on a plate in Seba (1734, vol. 1, pl. 72, fig. 4)].

*Hyla venulosa*—Daudin, 1803:71.

*Hyla zonata* Spix, 1824:41 [type formerly in ZSM, now lost, from Lago Tefé, Amazonas, Brasil; collector unknown].

*Hyla bufonia* Spix, 1824:42 [type formerly in ZSM, now lost, from Eca (= Tefé), Amazonas, Brasil; collector unknown].

*Hyla vermiculata* Duméril and Bibron, 1841:563 [holotype, MNHN 4797 from "Amérique Sept."; presented by Mr. Harlan].

*Phrynohyas zonata*—Fitzinger, 1843:30.

*Acrodytes venulosa*—Fitzinger, 1843:30.

*Hyla lichenosa* Günther, 1859 [lectotype, BMNH 1936.12.3.119 from Amazonas, Brasil; collector unknown].

*Scytotis hebes* Cope, 1862:354 [holotype, USNM 5837 from "Paraguay" (restricted to Asunción by Duellman, 1956:16); T. J. Page collector]. New synonymy.

*Scytotis venulosus*—Cope, 1866:85.

*Hyla spilomma* Cope, 1877:86 [holotype, unknown, apparently lost, from Cosamaloapam, Veracruz, México; Francis Sumichrast collector].

*Hyla paemulata* Brocchi, 1879:21 [holotype, formerly in MNHN, now lost, from western (= southern?) Guatemala; collector unknown].

*Hyla nigropunctata* Boulenger, 1882:366 [syntypes, BMNH 59.9.20.2 and 81.10.31.20 from Jalapa, Veracruz, México; Alphonse Hoeg collector].

*Hyla palpebrogranulata* Andersson, 1906:14 [holotype, ZIUS A133 from Tatarenda, Santa Cruz, Bolivia; Erland Nordenskiöld collector]. New synonymy.

- Hyla resinifictrix* Goeldi, 1907:135 [holotype, BMNH 1947.2.23.24 from San Antonio do Prata, Pará, Brasil; Emil Goeldi collector].
- Hyla zernyi* Ahl, 1933:27 [holotype, NHMW 16503 from Taperinha, near Santarém, Pará, Brasil; H. Zerny collector]. New synonymy.
- Hyla zeryni* Ahl, 1933:27 [holotype, NHMW 16503 from Taperinha, near Santarém, Pará, Brasil; H. Zerny collector]. New Synonymy.
- Acrodytes inflata* Taylor, 1944:63 [holotype, FMNH 100046 from La Venta, Guerrero, México; Edward H. Taylor collector].
- Acrodytes spilomma*—Taylor, 1944:64.
- Acrodytes modesta* Taylor and Smith, 1945:594 [holotype, USNM 115013 from Cruz de Piedra, near Acacoyaqua, Chiapas, México; Hobart M. Smith collector].
- Hyla macrotis* Andersson, 1945:70 [holotype, NHRM 1958 from the Río Pastaza watershed, Ecuador; William Clarke-MacIntyre collector]. New synonymy.
- Phrynohyas hebes*—Duellman, 1956:16.
- Phrynohyas inflata*—Duellman, 1956:19.
- Phrynohyas ingens* Duellman, 1956:22 [holotype, UMMZ 55570 from La Fría, Pueblo Nuevo, Zulia, Venezuela; H. B. Baker collector]. New synonymy.
- Phrynohyas latifasciata* Duellman, 1956:24 [holotype, BMNH 83.2.7.1 from Presidio, Sinaloa, México; Alfonso Forrer collector].
- Phrynohyas modesta*—Duellman, 1956:25.
- Phrynohyas spilomma*—Duellman, 1956:28.
- Phrynohyas corasterias* Shannon and Humphrey, 1957:15 [holotype, UIMNH 67060 from 4.8 miles east of San Blas, Nayarit, México; Francis L. Humphrey and Frederick A. Shannon collectors].
- Phrynohyas venulosa*—Hemming, 1958:172.
- Hyla tibiatrix tibiatrix*—Rivero, 1961:127.
- Hyla tibiatrix ingens*—Rivero, 1961:131.
- Hyla venulosa venulosa*—Rivero, 1964:493.
- Hyla adenoderma* Lutz, 1968:3 [holotype, MNRJ 4054 from Rio Branco, a tributary of the Rio Madeira, Rondonia, Brasil; F. Casper collector]. New synonymy.

*Distribution*.—In South America—the Caribbean lowlands, including Trinidad and Tobago, the Amazon Basin, the Chaco, and northeastern Brasil (Fig. 1). Only one specimen is known from the Pacific lowlands; Duellman (1956:42) reported that specimen as being from Hacienda San Miguel, Milagro, Guayas Province, Ecuador, but James A. Peters, the collector, informed me that it actually came from 7 kilometers southeast of Buenavista, El Oro Province, Ecuador. All specimens are from elevations of less than 800 m. 475 specimens from 107 localities.

*Remarks*.—This widespread, variable species has received 19 names in 200 years. The earliest name, *Rana venulosa* Laurenti, 1768, was based on a plate in Seba's "Thesaurus" (1734). Type specimens of *Hyla zonata* Spix, *H. bufonia* Spix, *H. spilomma* Cope, and *H. paenulata* Broechi are no longer extant. I have examined the types of the other 14 nominal species. Duellman (1961) provided evidence that *P. corasterias* Shannon and Humphrey, 1957, was not specifically distinct from *P. inflata* (Taylor, 1944). Duellman (1966) showed that *P. modesta* (Taylor and Smith, 1945) was a color morph

of *P. spilomma* (Cope, 1877). McDiarmid (1968) analyzed variation in Middle American *Phrynohyas* and concluded that *P. spilomma* (Cope, 1877), *P. inflata* (Taylor, 1944), and *P. latifasciata* Duellman, 1956, were synonymous with *P. venulosa* (Laurenti, 1768). My recent studies (Duellman, 1970) support McDiarmid's conclusions; all Middle American populations seem to be correctly allocated to *Phrynohyas venulosa*.

Of the names in the foregoing synonymy, Duellman (1956) listed *Hyla vermiculata* Duméril and Bibron, *H. lichenosa* Günther, and *H. resinifictrix* Goeldi in the synonymy of *Phrynohyas zonata* (Spix) [= *P. venulosa* (Laurenti)]. Duellman (1956) included *Hyla nigropunctata* Boulenger in the synonymy of *Phrynohyas spilomma* (Cope), now considered to be a synonym of *P. venulosa* (Laurenti).

Duellman (1956) distinguished *Phrynohyas hebes* from *venulosa* by the wider dark limb bands in the former. Examination of additional material from throughout the range of *venulosa* and especially from Argentina, Bolivia, Paraguay, and southern Brasil reveals that the supposed differences between *venulosa* and *hebes* are not constant. Thus, I now consider *Scytopsis hebes* Cope, 1862, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

Duellman (1956) distinguished *Phrynohyas ingens* from *venulosa* chiefly on the basis of the larger size of the former and by its dorsal coloration consisting of small brown spots on a tan ground color, as opposed to a large dark blotch on the dorsum in *venulosa*. It is now apparent that the coloration considered to be diagnostic of *ingens* appears in populations throughout most of the range of *venulosa* (Table 2). Furthermore, the size of *ingens* is equaled or exceeded by some individuals from Ecuador and Costa Rica. Consequently, I now consider *Phrynohyas ingens* Duellman, 1956, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

The holotype of *Hyla vermiculata* Duméril and Bibron (MNHN 4797) is an adult male having a snout-vent length of 65.2 mm. The specimen is soft and has been abraded. The dorsum is medium brown with distinct reddish brown marks; dark marbling is evident on the flanks and posterior surfaces of the thighs. The remnants of the color pattern are reminiscent of one of the color morphs of *Phrynohyas venulosa* common in northeastern South America.

*Hyla lichenosa* Günther was based on several juveniles; Smith and Taylor (1948:75) designated BMNH 1936.12.3.119 as the lectotype. This specimen has the usual tuberculate skin of young *Phrynohyas*, and it has a color pattern resembling that of young *P. venulosa* from Belém, Pará, Brasil.

The holotype of *Hyla resinifictrix* Goeldi (BMNH 1947.2.23.24) is a male having a snout-vent length of 75.3 mm. The color pattern is well preserved. The ground color is golden tan; anteriorly, on the dorsum, there is a reddish brown blotch, which is narrowly separated from a large, posterior blotch. The limbs bear distinct cross bars; the skin on the dorsum is distinctly pustulate. In features of structure and coloration the holotype is like most individuals of *P. venulosa* from the lower Amazon Basin.

The holotype of *Hyla palpebrogranulata* Andersson (ZIUS A133) is a juvenile having a snout-vent length of 32.3 mm. The skin on the dorsum is tubercular. The dorsum is yellowish tan with a large brown blotch beginning on the head and extending nearly to the vent. Broad brown cross bars are present on the limbs. A pair of pigment clusters above the anal opening suggest that the specimen is a recently metamorphosed young. The iris has the markings characteristic of *P. venulosa*; broad black streaks radiate from the pupil. This juvenile specimen certainly is a *Phrynohyas venulosa*. Cochran and Goin (1970) recognized a monotypic "*Hyla palpebrogranulata* group." I have examined all of the Colombian specimens that they referred to *H. palpebrogranulata* and find that all are young *Osteocephalus taurinus*.

The holotype of *Hyla wettsteini* Ahl (NHMW 19013) is a female having a snout-vent length of 61.3 mm and a moderately tuberculate dorsum. The dorsal surfaces of the head, body, and limbs are pale brown with scattered small brown spots (Fig. 2c). The pattern is identical to that of many individuals of *P. venulosa* from the middle and upper Amazon Basin and from Venezuela and Guyana.

The holotype of *Hyla zernyi* Ahl (NHMW 16503) is a juvenile having a snout-vent length of 20.4 mm and only slightly tubercular skin on the dorsum. The dorsum is pale tan with a narrow, elongate brown blotch beginning on the eyelids and extending to the sacrum. The flanks are brown, and the limbs are marked with irregular dark brown cross bars. The upper lips are boldly marked by three vertical bars, the first two of which fuse with a broad, diffuse canthal stripe, whereas the third enters the orbit. A broad, postorbital brown stripe encompasses the tympanum and is confluent with the dark flanks. The edge of the lower jaw is dark brown interrupted by creamy white spots. In structure, this specimen is like juvenile *P. venulosa*; the color pattern is bold but falls within the range of variation of *P. venulosa*.

The holotype of *Hyla macrotis* Andersson (NHMR 1958) is an adult female having a snout-vent length of 110.2 mm. The skin on

the dorsum is thick and glandular; the parotoid glands are extensive, diffuse, and form a moderately heavy supratympanic fold. The dorsum is uniform reddish brown; the loreal region is slightly paler brown, and the tympanum and groin are pale cream. The dentigerous processes of the prevomers are nearly transverse elevations between the choanae and bear 10-10 teeth. Specimens resembling the type have been examined from several localities in Amazonian Ecuador; some of these have small dark spots on the dorsum and thus resemble the smaller spotted color morph known from Amazonian Brasil, Perú, and Bolivia. One of the large *macrotis*-like frogs was prepared as a skeleton; no osteological differences between that specimen and several of *P. venulosa* were apparent. Consequently, *Hyla macrotis* Andersson, 1945, is considered to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

The holotype of *Hyla adenoderma* Lutz, 1968 (MNRJ 4054) is a female having a snout-vent length of 66.0 mm. The skin on the dorsal surfaces of the head and body is greatly thickened and glandular, more so than in any other specimen of *Phrynohyas* that I have seen. The dorsal color pattern consists of a network of bold dark brown reticulations on a tan ground color (Lutz, 1968, fig. 1); dark brown cross bars are evident on the limbs. The following data supplement Lutz's description: The discs on the hands are large and equal in diameter to the tympanum, the upper edge of which is covered by a heavy supratympanic fold. There are 7-9 prevomerine teeth on narrowly separated transverse elevations between the choanae. Although the iris is faded, there is a faint indication of radiating black streaks. This specimen seems to represent an extreme in glandular development of the skin and of a bold reticulated pattern. Otherwise, it is unquestionably a *P. venulosa*. Individuals having a fainter reticulated pattern are known from various localities in the Amazon Basin and Guianas. One specimen from Leticia, Colombia (KU 126067), has dorsal skin nearly as thick and glandular as that of the type of *Hyla adenoderma*, but the Colombian specimen has a large divided blotch on the dorsum. I consider *Hyla adenoderma* Lutz, 1968, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

## SUMMARY

*Phrynohyas* is one of four genera in the Hylidae having paired lateral vocal sacs behind the angles of the jaws; the other genera are *Argenteohyla*, *Osteocephalus*, and *Trachycephalus*. The four species of *Phrynohyas* exhibit differences in size, external structural

features, coloration, and cranial osteology. *Phrynohyas venulosa* is widespread in the tropical lowlands from northern México to northern Argentina; the other three species have much more restricted distributions—*P. coriacea* in Surinam and the upper Amazon Basin, *P. mesophaea* on the coastal lowlands of southeastern Brasil, and *P. imitatrix* in the uplands of the coastal ranges of southeastern Brasil. Only *P. coriacea* and *venulosa* are known to occur sympatrically.

The variability in size, coloration, and texture of the skin on the dorsum in *P. venulosa* has resulted in 19 specific names being proposed for this species. Seven nominal species are herein relegated to the synonymy of *Phrynohyas venulosa* (Laurenti, 1768); these are: *Scytopsis hebes* Cope, 1862; *Hyla palpebrogranulata* Andersson, 1906; *Hyla wettsteini* Ahl, 1933; *Hyla zernyi* Ahl, 1933; *Hyla macrotis* Andersson, 1945; *Phrynohyas ingens* Duellman, 1956; and *Hyla adenoderma* Lutz, 1968. *Hyla quadrangulum* Boulenger, 1882, is placed in the synonymy of *Phrynohyas coriacea* (Peters, 1867).

## RESUMEN

*Phrynohyas* es uno de cuatro géneros en la familia Hylidae que poseén sacos vocales laterales apareados, localizados detrás de los ángulos de las articulaciones mandibulares; los otros géneros son: *Argenteohyla*, *Osteocephalus*, y *Trachycephalus*. Las cuatro especies de *Phrynohyas* exhiben diferencias en tamaño, rasgos estructurales externos, coloración, y osteología cranial. *Phrynohyas venulosa* está ampliamente distribuida en las tierras bajas tropicales, desde el norte de México al norte de Argentina; las otras tres especies tienen distribuciones más restringidas—*P. coriacea* en Surinam y la parte alta de la cuenca amazónica, *P. mesophaea* en las tierras bajas de la costa del sureste del Brasil, y *P. imitatrix* en las tierras altas que costean el sureste brasileño. Se sabe, que sólo *P. coriacea* y *venulosa* ocurren simpatricamente.

Diez y nueve nombres especificados han sido propuestos para *P. venulosa*, debido a la variabilidad del tamaño, coloración, y textura de la piel dorsal de esta especie. Siete especies nominales son relegadas aquí a la sinonimia de *Phrynohyas venulosa* (Laurenti, 1768); estas son: *Scytopsis hebes* Cope, 1862; *Hyla palpebrogranulata* Andersson, 1906; *Hyla wettsteini* Ahl, 1933; *Hyla zernyi* Ahl, 1933; *Hyla macrotis* Andersson, 1945; *Phrynohyas ingens* Duellman, 1956; y *Hyla adenoderma* Lutz, 1968. *Hyla quadrangulum* Boulenger, 1882, es puesta en la sinonimia de *Phrynohyas coriacea* (Peters, 1867).



## SPECIMENS EXAMINED

The localities for each of the specimens examined are given below. The arrangement of the data is as follows: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museum, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed first in the most restricted political unit possible; localities which have not been found on maps or which are too vague to be located precisely are given in quotation marks. Where more than one specimen is included under one museum number, the number of specimens is given in parentheses after the museum number. Unless noted otherwise, all specimens are preserved in alcohol.

*Phrynohyas coriacea*

ECUADOR: "western Ecuador," BMNH 1947.2.13.75. *El Oro*: Machala, WCAB 40100. *Napo*: Lago Agrio, KU 126656; Limón Cocha, KU 107025, UIMNH 87799, 90315-6; Santa Cecilia, KU 105249, UMMZ 129323. *Pastaza*: "Río Pastaza watershed," NHRM 1950 (7).

PERÚ: *Loreto*: Pebas, CAS-SU 12622; Puerto Oriente, 5 km. above Contamana, Río Ucayali, UMMZ 123915.

SURINAM: No specific locality, BMNH 70.3.10.69, ZMB 5807 (3); "Sporoban," RMNH 9606. *Marowijne*: Albino, Río Maroni, ZMB 7606 (3); Maroni, ZMB 7605 (2); Nassaugeberge, RMNH 7296.

*Phrynohyas imitatrix*

BRASIL: *Rio de Janeiro*: Teresópolis, MNHN 31/45-46, NHMW 18433.5, SMF 58269. *Santa Catarina*: Río Vermelho, KU 92249 (skeleton), 92250-1. *São Paulo*: São José do Barreiro, Serra da Bocaina, SMF 62562.

*Phrynohyas mesophaea*

BRASIL: No specific locality, UZM 14223, ZMB 3122. *Bahia*: Santa Cruz, ZMB 30444. *Guanabara*: Río de Janeiro, KU 92252-6, 92257 (skeleton), SMF 30024-9. *Rio de Janeiro*: Angra dos Reis, ZSM 60/1947; "Guapy," SMF 39251-3; 36 km from Río Petrópolis road, BMNH 1940.4.14.13; Teresópolis, SMF 2515, ZMB 26322. *Rio Grande do Sul*: Porto Alegre, ZMB 6256, 6810. *Santa Catarina*: No specific locality, UZM 14224; Blumenau, NHMW 6279-80; Hansa (= Corupá), BMNH 1928.11.5.89-106, SMF 2500-14, 30998, 31001-27; Jaraguá, NHMW 6293 (4); Joinville, MNHN 6310 (5), NHMW 6282-3, 6287 (4), 6288 (21), 6289 (2), 6290 (6), 6291 (5), 6294 (5), 6295 (7), 6296 (6), 6297 (5), 6298 (6), 6299 (9), 6300 (6), 6301 (6), 6302 (7), 6303 (4), 6304 (3), 6305 (3), 6306 (7), 6307 (9), 6309 (3), SMF 2516-34, 5120, 5131; "Río Humboldt," BMNH 1910.7.26.3-6, 1923.6.1.84-91; "Río Novo," NHMW 6286 (5), 6295 (5).

*Phrynohyas venulosa*

AMERICA: No specific locality, MNHN 4797.

ARGENTINA: No specific locality, USNM 73523. *Chaco*: Ciervo Petizo, KU 128948-50; Colonia Eliza, NHRM 1503. *Entre Ríos*: Puerto Marquez, 2 km N La Paz, SMF 43634. *Salta*: Río Pescado, KU 128946-7.

BOLIVIA: No specific locality, NHMW 6177 (3). *Cochabamba*: Río Chaparé, ZSM 9/1948. *El Beni*: Esperanza, BMNH 1920.11.29.15-16; Rer-

renabaque, UMMZ 57528, 57531 (2). *La Paz*: Ixiamas, MCZ 10087, UMMZ 57529 (4), 57530 (3); Santa Ana de Movimas, BMNH 98.6.9.38. *Santa Cruz*: Buenavista, BMNH 1927.8.185-6, CM 2582, 3828, 3892-3, 3971, 3974, 3986, 4467-8, UMMZ 60526, 63960 (2), 66559-60; Río de la Cal, ZMB 32107; Santa Cruz, BMNH 1904.10.29.177, 1907.10.31.72, 1927.8.1.87, CM 2514; Tatarendá, ZIUS A133.

BRASIL: "lower Amazonia," USNM 28926-7. *Amazonas*: No specific locality, BMNH 1936.12.3.119; Aiapuá, ZMB 30303; Fonte Boa, NHMW 6104; Manacapuru, Río Solimões, ZMB 37080, ZSM 23/1924; Manáas, AMNH 51755, IRSNB 2681 (14), KU 92258-61, UMMZ 66647; Río Caicara, NHMW 6111 (2), 6119 (2), 13262 (2); Río Juruá, BMNH 1904.11.4.12; Río Purús, ZMB 30307; Tefé, NHMW 6100. *Bahia*: No specific locality, BMNH 64.1.19.34, NHMW 6281. São Gonçalo, 30 km SW Feira de Santana, KU 29438, MCZ 1531. *Mato Grosso*: Barro do Tapirapé, CAS-SU 12304-10, 12312, KU 40219; Chapada dos Guimarães, BMNH 1903.3.26.54-6; Posto Jacarú, Río Xingú, KU 92262-3; Villa Murinho, UMMZ 56770. *Minas Gerais*: La Filomena, NHMW 6102 (2), 6112 (2), 6114 (3), 6115; Manga, Río São Francisco, UMMZ 108894; Piraporinha, USNM 98536-7; São Luís dos Caceres, CAS-SU 12298-9. *Pará*: Belém (= Pará), BMNH 45.8.25.143, 96.1.7.2, CAS-SU 12390-3, NHMW 6098, ZMB 33189, ZSM 119/1911 (2); Cachoeira de Arari, Ilha de Marajó, ZMB 29999, ZSM 120/1911; Cametá, Río Tocantins, NHMW 6099, 6107, 6113; "Ilha de Marajó," BMNH 1923.11.9.26; IPEAN, 3 km E Belém, KU 127963-4, 128557-61, 130121-6; Livramento, CAS-SU 12383-7; "San Antonio do Prata," BMNH 1947.2.23.24; Santarém, BMNH 56.3.25.14 (2); Taperinha, near Santarém, NHMW 16503, 19013. *Pernambuco*: No specific locality, BMNH 58.11.28.48; Bonita, MCZ 4998. *Piani*: Bosques, BMNH 1926.5.26.4. *Rondonia*: Río Branco, MNRJ 4054. *Roraima*: Serra Grande, below Boa Vista, Río Branco, NHMW 15893.

COLOMBIA: *Amazonas*: Leticia, KU 124897-900, 124955-6 (tadpoles); 2 km E Leticia, KU 126067. *Caquetá*: Morelia, ANSP 25313. *Cundinamarca*: Honda, MLS 1-2. *Magdalena*: Barranquilla, MLS 3; Fundación, UMMZ 48263. *Norte de Santander*: Río Zulia, N of Cucutá, MLS 4.

ECUADOR: No specific locality, USNM 14054. *El Oro*: 7 km SE Buenavista, USNM 192507. *Napo*: Avila, USNM 165979-80; Lago Agrio, KU 126657; Río Cotapino, KU 138736, USNM 165977-8. *Pastaza*: Montalvo, CAS-SU 10318-9, USNM 165981 (skeleton), 165982-3; Río Bobonaza, USNM 165984; upper Río Oglán, USNM 165986; "Río Pastaza watershed," NHRM 1958; Río Villano, USNM 165988.

FRENCH GUIANA: *Cayenne*: Cayenne, BMNH 53.2.89-90, NHMW 6101, 6103; Mt. Cabasson, LACM 44638.

GUYANA: *East Demerara*: Georgetown, MCZ 2618, UMMZ 80495. *Essequibo*: Better Hope, BMNH 80.11.22.5-6. *Mazaruni-Potaro*: Kaieteur Falls, AMNH 23128. *North West*: Santa Rosa Island, Moruka River, UMMZ 55834. *Rupununi*: north of Acaray Mts., west of New River, KU 69778-82.

PARAGUAY: No specific locality, AMNH 19916-7, 19919, USNM 5837; "Alto Paraguay," ZMB 26181. *Boquerón*: Loma Plata, KU 73432. *Central*: Asunción, BMNH 94.3.14.168; Patiño, FMNH 10799. *Concepción*: Apa-Bergland, ZSM 137/1933. *La Cordillera*: San Bernardino, NHMW 6106 (2), ZMB 26054, 26115. *Olimpo*: Puerto 14 de Mayo, Bahía Negra, BMNH 98.6.3.19.

PERÚ: *Loreto*: "Caseirio Libertad, Río Amazonas," MJP 514; Orellana, USNM 127168-9, 127180; Pebas, CAS-SU 3159, 6376, 12622; Pucallpa, MJP 84, 86 (3), 90, 92, 93 (2), 95, 97 (2), 99; Río Ucayali, FMNH 3562, UMMZ 48210; Roabaya, AMNH 43316, 43534; "Transval, near Pebas," CAS-SU 3162.

SURINAM: No specific locality, BMNH 70.3.10.68-9, NHMW 6097, 6109 (2), USNM 14618. *Brokopondo*: Brokopondo, RMNH 16692 (2). *Coronie*: Coronieweg, RMNH 16693. *Marowijne*: Camp 3, RMNH 16694. *Suriname*:

Berg en Dal, ZMB 7267; Coropina Creek, RMNH 16695; Kwattaweg, RMNH 16696; "Lelydorp," RMNH 16697 (2); Paramaribo, AMNH 4009, ANSP 2169-70, BMNH 1946.4.2.24-25, MCZ 7662, RMNH 16698 (9), USNM 13820-1, ZMB 25966 (2), 26076.

TRINIDAD AND TOBAGO: *Tobago*: Milford Bay, MCZ 4087; "Whim," BMNH 1926.1.19.1. *Trinidad*: No specific locality, FMNH 41683, MCZ 3517, 5971; "Churchill-Roosevelt Hwy," AMNH 55712-15 (16), 55717-19; "Cumpia," SMF 2646-47; Fyzabad, BMNH 1929.11.25.6; "Imperial College of Agriculture," BMNH 1932.9.16.41; "Mt. Harris," FMNH 49701; "Mt. Tabor," CM 5257; "Oarino River," BMNH 1929.11.25.4; "Piarco," KU 84714; "St. Augustine," AMNH 55716.

VENEZUELA: "Los Canales," USNM 128792. Anzoátequi: Carapa, USNM 80612. *Aragua*: Maracay, ZSM 304/1929 (20), 305/1929 (46), 61/1930 (22), 120/1930 (4), 292/1933 (6), 43/1934 (10), 105/1935 (11), 196/1965 (5). *Distrito Federal*: Caracas, SMF 2645; La Guaira, USNM 22545, 27797. *Monagas*: Caicara, AMNH 16904-6, 16911-2, USNM 36377; Caripito, USNM 117098-9. *Trujillo*: Savana de Mendoza, UMMZ 57397. *Zulia*: La Fría, Pueblo Nuevo, UMMZ 55567-70; Oropé, FMNH 2604.

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